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ECOLOGY OF KENTUCKY FLOWERS: II. THE FIFTH STAMEN OF PENTSTEMON CANESCENS BRITTON [1]

By Harvey B. Lovell

The sterile fifth stamen of *Pentstemon,* or beard's tongue, long has been the subject of much controversy among ecologists. There is no more unusual structure to be found in the whole figwort family. At least six different ideas have been proposed to explain the function of this curious hairy tuft. These range all the way from that of a landing platform and nectar guide to a useless or inimical vestige.

Since *Pentstemon canescens* Britton, a species not heretofore studied, grows abundantly in Jefferson County, Kentucky, it was decided to attempt further observations with a view to ending the controversy. Insects were collected from one patch of about an acre located along a drainage ditch. A second plot was discovered which extended over 20 acres and which was covered with a nearly solid stand of the plants. The identification of the species was kindly checked by L. B. Smith of the Gray Herbarium.

The flowers are white, often with a purplish tinge, and are borne in compound inflorescences (Fig. 4A) producing an average of 90 flowers. Since each flower is from 20 to 23 mm. in length, the flower clusters are very conspicuous at least to the human eye.

The tubular portion of the corolla is about 18 mm. long, and consists of a slender basal portion 8 mm. long which flares into an expanded chamber 10 mm. long and 6 to 7 mm. high. The lower lip of three segments forms an excellent landing platform for insects and is marked by purple lines, the nectar-guides.

The sterile stamen, or staminodium, arises from the upper side of the corolla and bends down across the tube with its distal end coming to rest on the floor of the vaulted chamber (Fig. 4B).

[1] Contribution from the Department of Biology of the University of Louisville.

The apical 6mm. of the stamen are bearded with 8 to 10 long stiff, yellow hairs on the sides and numerous short brownish ones on the upper surface.

The four fertile stamens bend upward so that their anthers lie just beneath the upper lip in two sets, the lower pair being outermost. The anther cells dehisce longitudinally, exposing the pale straw-colored pollen which clings to the inside of the sacs (Fig. 4E). Their edges are provided with minute spines which help shake out the pollen as visiting insects rub against them.

The flowers are protandrous. When they first open the stigma lies above the four anthers. At this time the flowers are in the staminate stage, (Fig. 4B) the anthers having dehisced as the flowers opened. The stigma is glutinous even at this stage, but considering its out of the way position, it is doubtful if pollen comes into contact with it frequently.

The second or pistillate stage (Fig. 4C) follows in a day or two. At this time the style is bent downward abruptly near the tip, placing the stigma in a prominent place near the center of the flower. Meanwhile, most of the pollen has been removed from the anthers. Measurements of a number of pistils indicate that there is a slight lengthening (about 1 mm.) of the style as the pistillate stage is reached.

The flowers have a sweetish odor. Nectar is secreted by the expanded bases of the two upper filaments. The nectary thus formed occupies 1:5 mm. of the filament (Fig. 4D). Considerable nectar is secreted, but in most cases it remains in the upper side of the corolla tube (see dotted area on Fig. 4D). It could be tasted in many flowers. This species is undoubtedly of considerable value to bee-keepers for the flowers are extensively visited by honeybees.

As mentioned above, the most controversial feature of the flowers of the genus *Pentstemon* is the hairy sterile stamen. William Ogle (1870) has said that it would be better if this stamen had been entirely suppressed, and supposed that by lying on the lower surface of the flower it leaves room for the stigma and anthers in the upper part of the flower.

Pasqual (1895) considered that the hairy staminodium with a broadened end possessed by *P. gentianoides* is an organ for catching the pollen which drops from the anthers. Self-pollination fol-

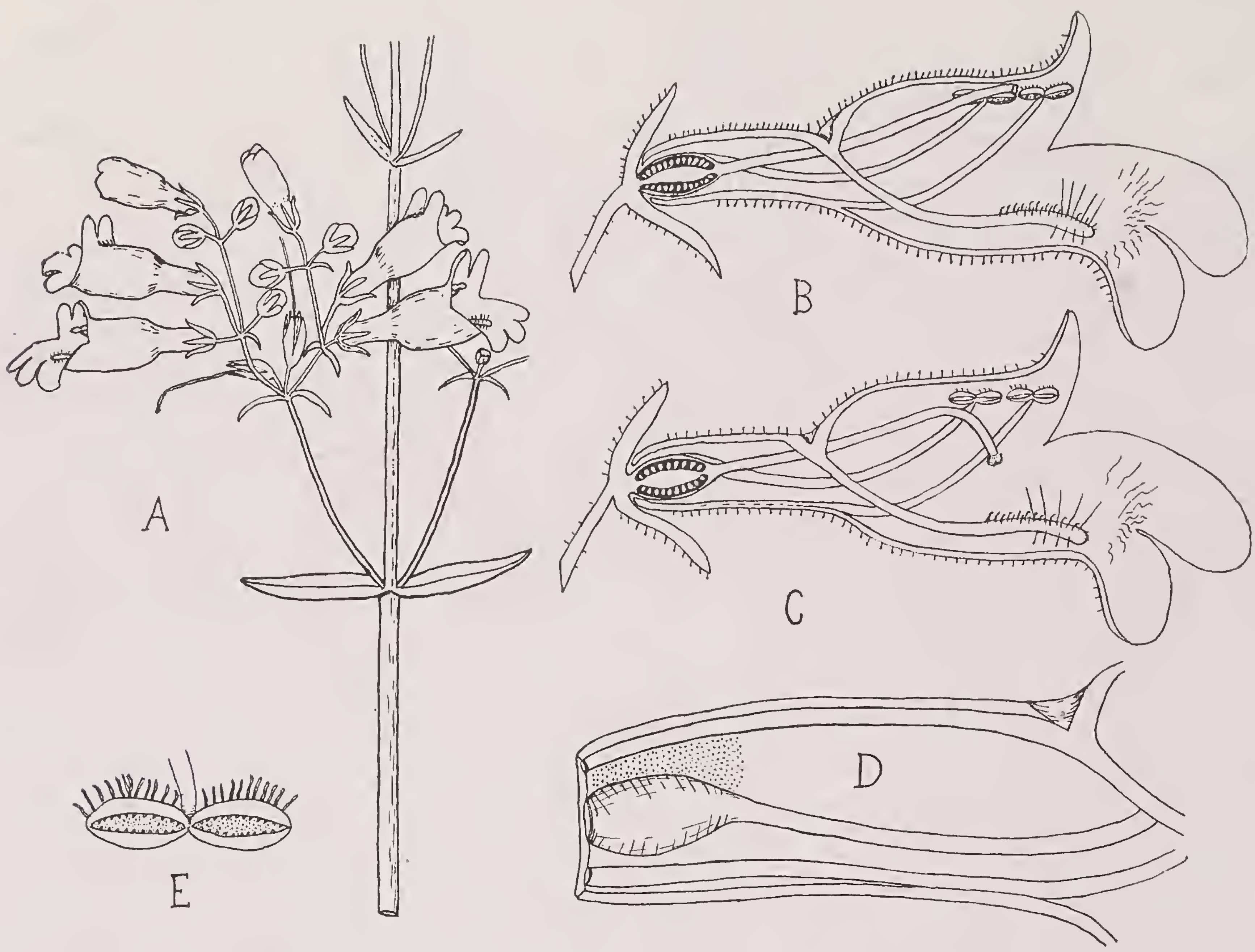

Figure 4, **Pentstemon canescens.** A. Part of an inflorescence, x 2/3; B. staminate stage, x 2; C. pistillate stage, x 2; D. corolla tube showing location of nectary and position occupied by nectar (dotted) x 6; D. an anther, x 8.

lows either by spontaneous movements which bring the sterile stamen and stigma together or by the aid of insects.

The most usual explanation, first suggested by Kerner and elaborated by Errera (1878), is that the staminodium partially closes the opening to the narrow portion of the corolla tube, and thus protects the nectar from short-tongued insects which would not touch the fertile organs as they crept into the flower.

In the case of *P. pubescens* Ait., according to Robertson (1891), the sterile filament is unusually hairy and together with two longitudinal folds on the lower surface so nearly closes the corolla tube that insects are forced to suck the nectar from the mouth of the flower.

Errera removed the staminodium from 20 flowers and reported that insects visited them without apparent difficulty. He concluded that the hairs do not serve as supports for insects as had been suggested by Delpino, but that they might force an insect to stand upright and increase the chances of its rubbing against the fertile organs.

The Darwinian philosophy of many of these early writers which led them to look for a survival value in every structure has passed out with the modern concept of mutations. A mutation may or may not be useful. In allied species of *Pentstemon* the staminodium is sometimes nearly aborted, sometimes reduced to a hairless thread, sometimes expanded or coiled at the tip, seemingly without materially affecting the success of the species. In *Chelone* the flower structure is very similar except for the absence of the staminodium.

However, it seems likely that a structure as highly evolved as the hairy filament in *P. canescens* is of some service to the flower, even if this service is not indispensable. Before reading Errera's paper I had already come to the conclusion that the staminodium's chief value was in forcing insects to stand upright and thus cause them to rub their heads and thoraces vigorously against the fertile organs. Such a mechanism causes even small insects, such as some of the *Megachile*, to touch the anthers. In the closed flowers of *Chelone* only powerful insects can gain an entrance, and they are forced to touch the fertile organs in the roof. In *P. canescens* the floral tube of 18 mm. is so long that its base could not be reached by the tongue of medium-sized insects if its apex were too narrow

to admit their heads. The presence of the dilated chamber, however, allows entry of medium-sized insects and thus gives the flower a wider range of visitors. In seasons when the larger insects are scarce, a flower with such a mutation would be more apt to set seed than one with a tube slender throughout the whole length.

A mutation for the enlarged throat by itself, however, would allow many small insects to creep into the flower without touching the reproductive organs. This has been prevented in other genera in different ways, as for example, by the walking-beam mechanism in *Salvia* which places pollen on the back of the insect. In *P. canescens* the numerous hairs on the staminodium perform the same function. In competition with a flower lacking the mutation for a hairy staminodium, a typical *P. canescens* would have a distinct advantage and the less favored form would tend to become extinct.

It is true, as stated by numerous authors, that the staminodium also blocks the entrance to the constricted portion of the floral tube, but the space between the wall and the style is already too small to permit the ingress of any but the tiniest of insects. Many other genera of tubular flowers have mutated to produce hairy tubes which perform more simply the function of exclusion.

During the present study it was noted that insect visitors of *P. canescens* were numerous and consisted chiefly of the *Melissodes, Bombus,* and the honeybee. *Melissodes compta* seems to be the most natural pollinator in this vicinity. The honeybee, being only a recent importation, cannot be classed as a natural pollinator of our native flowers. In this case its tongue is too short (6 mm.) to reach the nectar effectively in a flower with an 8 mm. tube. However, since the nectar occupies 2 to 3 mm. of the tube, the honeybee is able to obtain part of it by thrusting its head as far as possible into the base of the tube.

The long-tongued *M. compta* readily reaches all the nectar. The movements of its tongue could be observed through the translucent corolla in favorable locations. This insect was observed to collect pollen by entering the flower upside down and rubbing the anther-sacs with its legs. Pollen-collecting individuals were noted to discriminate on the wing between flowers in the staminate and pistillate stages. They would fly to the mouth of a flower, hover there for a second, and then apparently, if no pollen was visible, fly on to

another flower. A check of flowers thus passed over showed that they were all in the pistillate stage. Some individuals of this bee visited a flower first for nectar and then withdrawing their heads long enough to turn upside down, revisited the same flower for pollen.

Two short-tongued bees of the genus *Agapostemon* were also observed collecting pollen by clinging upside down to the anthers.

Xylocopa virginica, the carpenter-bee, was seen to rob flowers by piercing the corolla tube above the nectaries with her maxillae. Three individuals were observed to puncture more than a hundred flowers without once trying to obtain nectar in the proper way. Many flowers were punctured separately above each nectary.

The following collection of 200 visitors was made on June 6, 7, 8, 10, and 18, 1940. Since the insects were collected as they appeared, the numbers indicate approximately the relative importance of each species in this locality. Unless otherwise indicated, all visitors were collecting nectar and assisting in pollination. Those collecting pollen are indicated by c. p., those collecting both nectar and pollen by c. n., c. p. Females are indicated by F, males by M.

Long-tongued bees.—EUCERIDAE: *Melissodes* (Anthedon) *compta* Cr. 49 F, c. n., c. p.; *Synalonia speciosa* Cr. 1 M; ANTHOPHORIDAE: *Anthophora abrupta* Say, 1M, 2F; MEGACHILIDAE: *Megachile mendica* Cr. 3 F; M. *brevis* Say 2 F; *Alcidamea truncata* Cr. 3 F; XYLOCOPIDAE: *Xylocopa virginica* Drury 3 F; BOMBIDAE: *Bombus americanorum* Fab. 15 F; *B. separatus* Cr. 5 F; *B. auricomus* Rob. 2 F; *B. impatiens* Cr. 1 F; APIDAE: *Apis mellifera* L. 109 workers.

Short-tongued bees.—HALICTIDAE: *Agapostemon radiatus* Say 1 F, c. p.; *A. virescens* F. 1 F, c. p.; *Halictus sp.* 2 F, c. p.

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